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RESEARCH ARTICLE

Temperature and circadian effects on metabolic rate of South American echimyid rodents, *Trinomys setosus* and *Clyomys bishopi* (Rodentia: Echimyidae)

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ABSTRACT. Basal metabolic rate (BMR) represents the lowest level of metabolic activity capable to sustain homeostasis in an endotherm and is an important tool to compare metabolic rates of different species. Echimyidae is the most specious family within caviomorph rodents, however, little is known about the biology of its species, such as *Trinomys setosus* (Desmarest, 1817) and *Clyomys bishopi* (Ávila-Pires & Wutke, 1981), a ground and an underground dwelling echimyid, respectively. The ambient temperature and circadian effects on metabolic rate were evaluated through closed-system respirometry for these two species, as well as the circadian effects on CO_2 production and respiratory exchange ratio (RER). *Trinomys setosus* and *C. bishopi* showed the lowest metabolic rates (0.56 ± 0.02 $mLO_2.h^{-1}.g^{-1}$ and 0.53 ± 0.03 $mLO_2.h^{-1}.g^{-1}$, respectively) at 32 °C and during the light phase. Under laboratory conditions, *T. setosus* showed metabolic rate variation compatible with nocturnal activity, whereas *C. bishopi* activity cycle remains unclear. Both species showed BMR lower than expected by allometric regressions for rodents.

KEY WORDS. Basal metabolic rate, fossoriality, neotropical, oxygen consumption, thermoneutral zone.

INTRODUCTION

Animals expend energy for numerous purposes such as maintenance of homeostasis, foraging, food digestion, growth, and reproduction. The timing of those activities is fundamental to increase survival. Deviations from the standard biological rhythm can be strongly selected against in nature (DeCoursey et al. 2000, Spoelstra et al. 2016) and most species will display activity cycles entrained to light and dark phases (Koukkari and Sothern 2006).

The basal metabolic rate (BMR) represents the lowest level of metabolic activity necessary to sustain homeostasis in endotherms (Hulbert and Else 2004, Careau et al. 2008), and has been an important tool to compare metabolic rates among different species (Hulbert and Else 2004). Although the BMR is widely used to answer physiological, ecological and behavioral questions, a reliable BMR measurement depends on ensuring that experimental trials were performed using an adult animal at rest in a postabsorptive (non-digestive) and non-reproductive state and in a thermoneutral environment (Hulbert and Else 2004).

Variations in BMR are mainly explained by body mass (Kleiber 1932), but many other factors may relate to BMR variation such as climate (Lovegrove 2003) and ecological habits (McNab 2008). Although body mass and BMR are strongly related, a single scaling exponent has not been determined to date (Hulbert and Else 2004, Capellini et al. 2010). Nevertheless, fossorial mammals are believed to present lower than expected BMR for a given body mass (McNab 1966, 1979, Vleck 1979, 1981). Two hypotheses try to explain this reduced BMR, the thermal-stress hypothesis (McNab 1966, 1979) and the cost-of-burrowing hypothesis (Vleck 1979, 1981). The former assumes that BMR is reduced due to heat dissipation limitations underground, while the latter assumes that this feature is related to the high energetic costs of excavating tunnels for foraging. Nevertheless, fossorial rodents will display different strategies to cope with underground constrains and lower than expected BMR could have been selected by different environmental pressures. In *Octodon degus* Molina, 1782, net primary productivity explains the intraspecific BMR variation (Bozinovic et al. 2009). On the

other hand, net primary productivity is not a good predictor for BMR in fossorial rodents in general, and ambient temperature was pointed out as the major determinant of residual BMR variation among underground rodents (Luna et al. 2017).

Echimyidae is the most specious family within caviomorph rodents (Upham and Patterson, 2012); however, little is known about the biology of its species. *Trinomys setosus* (Desmarest, 1817) is known to be a ground dwelling echimyid, but the exact distribution within the endangered Brazilian Atlantic rainforest is unknown (MMA 2012). Echimyidae also includes *Clyomys*, a fossorial genus with only scarce physiological information available (Nowak 1999). *Clyomys bishopi* (Ávila-Pires & Wutke, 1981) is restricted to the Brazilian savanna – called Cerrado, and presents morphological features related to a fossorial habit, such as, well-developed claws on the forefeet and enlarged bullae in the cranium (Nowak 1999). The only physiological data available for *C. bishopi* is resting metabolic rate (Barros et al. 2004), however, neither species have data available regarding thermoneutral zone nor biological rhythmicity. BMR data of these two closely related species are therefore not available and could contribute to our knowledge of metabolic physiology of echimyid species. These data can also provide information about the relationship between metabolic rate and fossoriality in this representative rodent taxon (Fabre et al. 2012).

This study aims to report for the first time BMR, CO_2 production and the respiratory exchange ratio (RER) of *T. setosus* and *C. bishopi*. To achieve this, ambient temperature and circadian rhythm effects will be considered. We hypothesize that both species will present the lowest metabolic rate within the light phase, as echimyids are usually nocturnal (Emmons and Feer 1997), and that BMR of *T. setosus* will fit the expected from allometric relationships (see Kleiber 1932, McNab 2008), whereas *C. bishopi* will present a lower than predicted BMR due to its fossorial life style.

MATERIAL AND METHODS

Trinomys setosus (316.6 ± 29.1 g) was caught in Brazilian Atlantic rainforest (13°00'S, 38°01'W) and *C. bishopi* (348.3 ± 23.8 g) was caught in Savanna-like environment (Ecological Station of Itirapina: 22°14'S, 47°52'W). Animals were housed in plastic opaque cages (30 x 40 x 16 cm) and exposed to an inverted 12:12 light:dark cycle. Food (NUVILAB CR1) and water were provided *ad libitum*. Animal manipulation was carried out in accordance to the guidelines of American Society of Mammologists (Sikes and Ganon 2011) and current Brazilian laws for capture (SISBIO: 43334-1), handling and care of mammals in captivity (CEUA:13.1.866.53.3).

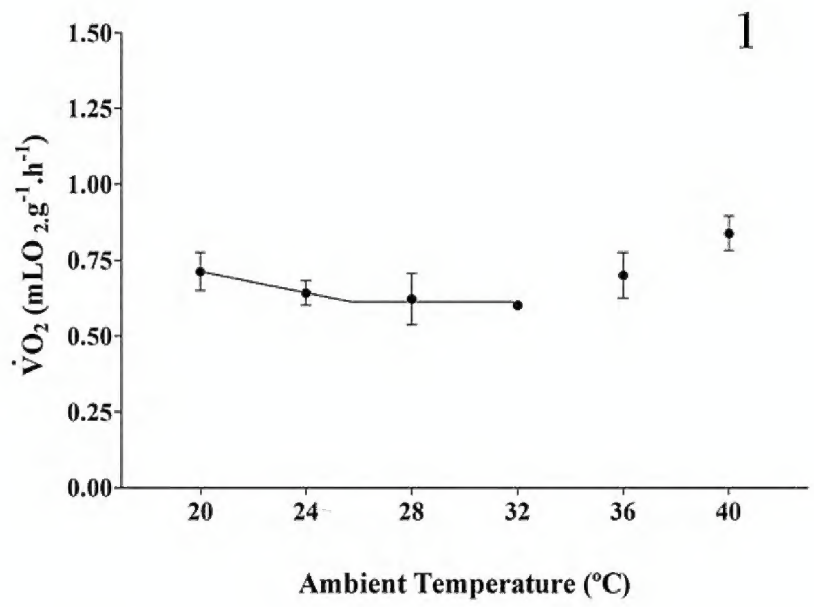
Oxygen consumption ($\dot{V}O_2$) and carbon dioxide production ($\dot{V}CO_2$) were obtained by a closed respirometry system (see Barros et al. 1998, Barros et al. 2004). Animals were individually kept inside a chamber (4.55L) within a temperature controlled cabinet (Q315F, QUIMIS). Measurements were conducted with chambers sealed for 10 minutes (600 samples) while circulating air samples through a CO_2 (CA-10A, Sable Systems) and an O_2 analyzer (PA-10, Sable System). CO_2 was measured during all experimental trials to ensure that CO_2 levels inside the chambers were below 1 %, a concentration unlikely to affect VO_2 measurements (Barros et al. 2004). Between measuring intervals, the chambers were flushed with room air using a high flow rate (≈ 1000 $mL.min^{-1}$). Animals were placed in the experimental apparatus three hours before experimental trials and were fasted for eight hours prior to measurements to ensure a post-absorptive state. To ensure acclimation, animals were previously submitted to experimental conditions two times with no measures recorded.

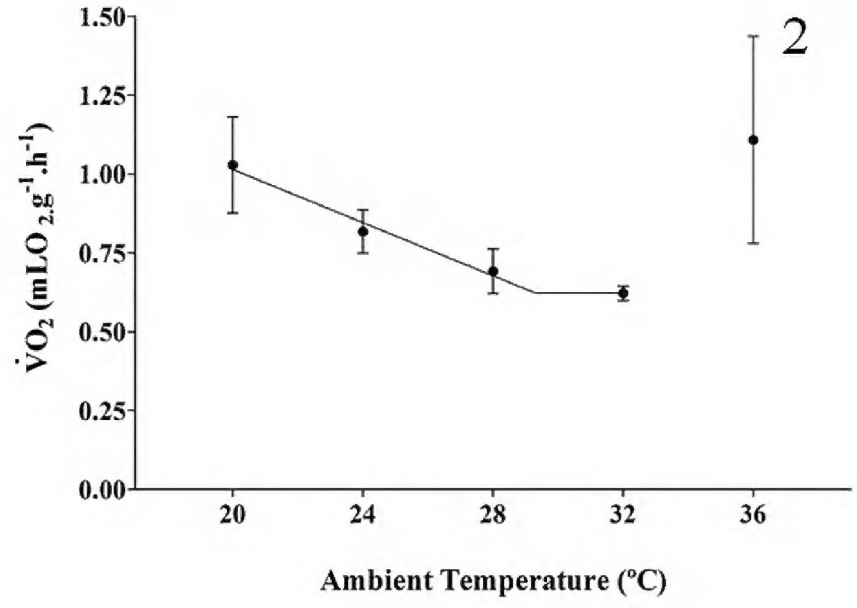
The same individuals were used in two experimental protocols to study the effects of ambient temperature (T_a) and circadian cycle on BMR. First, the effect of T_a on metabolic rate was evaluated through measurements of $\dot{V}O_2$ for each animal (N = 5) at T_a ranging from 20 to 40 °C for *T. setosus* and from 20 to 36 °C for *C. bishopi*, using 4 °C increments. Animals were acclimated at room temperature (25 °C) and experimental trials were conducted during the light phase in an attempt to minimize interference of other activities in the measurements taken. Animals were submitted to each T_a for 30 minutes and $\dot{V}O_2$ was determined on the last 10 minutes of each temperature exposure. Second, to access circadian effect on BMR, animals (N = 8) were measured in trials lasting 6 hours (starting in dark phase and ending in light phase), where each animal was measured every 40 minutes. Acclimation and experimental trials were conducted at the T_a indicated by the first protocol (32 °C, see Results). Circadian effects on $\dot{V}CO_2$ and RER are also reported.

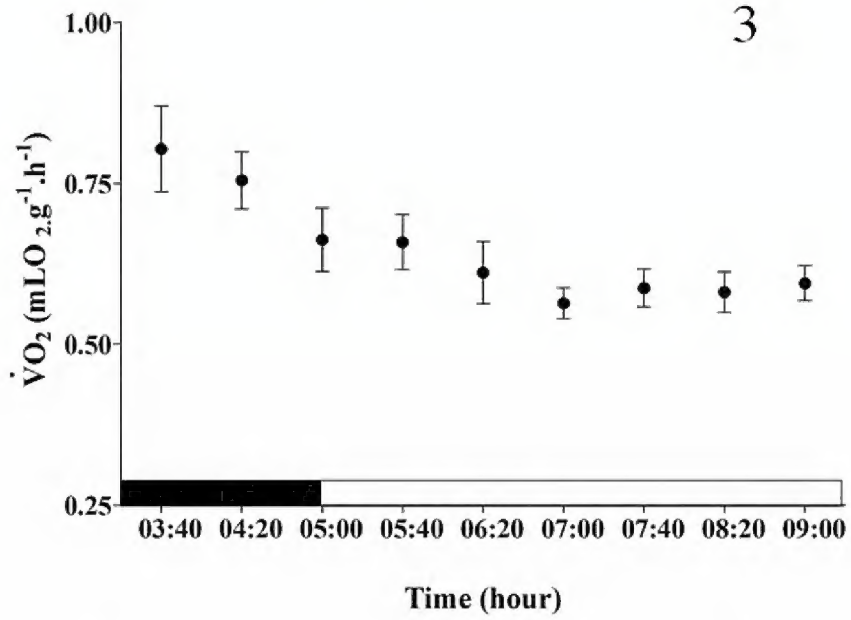
$\dot{V}O_2$ and $\dot{V}CO_2$ were obtained based on the regression of gas variation inside chambers and corrected to STPD. These two variables were used to calculate respiratory exchange ratio (RER). Segmented linear regression was used to evaluate the effects of T_a on metabolic rate. Among the different functions obtained, we selected the one that maximized the statistical coefficient of explanation (see Baldo et al. 2015). Circadian effect on $\dot{V}O_2$ was evaluated using an analysis of variance (repeated measures ANOVA, $\alpha = 0.05$) between the lowest $\dot{V}O_2$ of dark and light phases. $\dot{V}O_2$, $\dot{V}CO_2$ and RER measures of different daytimes were compared within the inactive phase (repeated measures ANOVA, $\alpha = 0.05$). All values represent mean and standard error (mean ± SE). Measures within the thermoneutral zone and during the inactive phase were considered to represent basal metabolic rate (BMR). Statistical analyses were conducted using PRISM 6 (GraphPad Software, San Diego, USA).

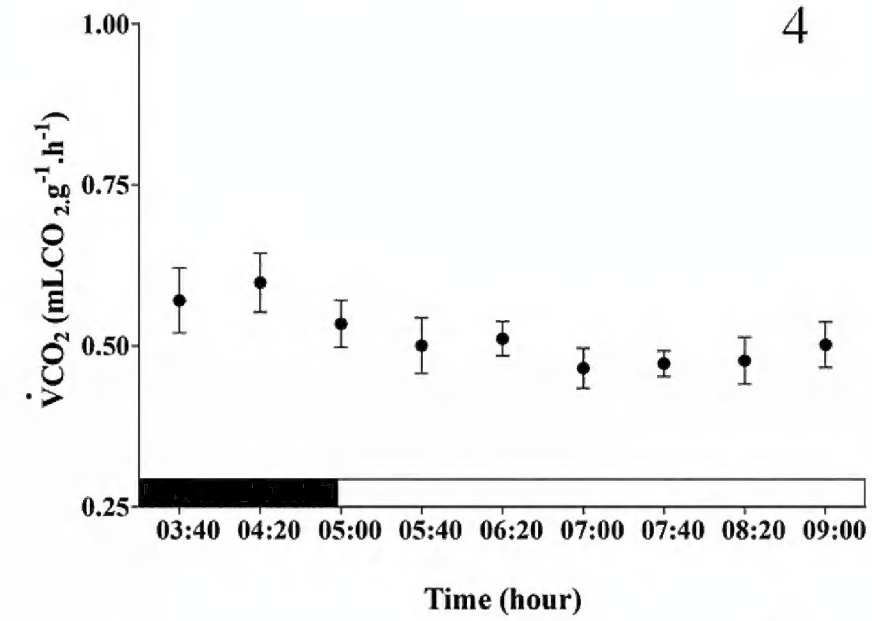
RESULTS

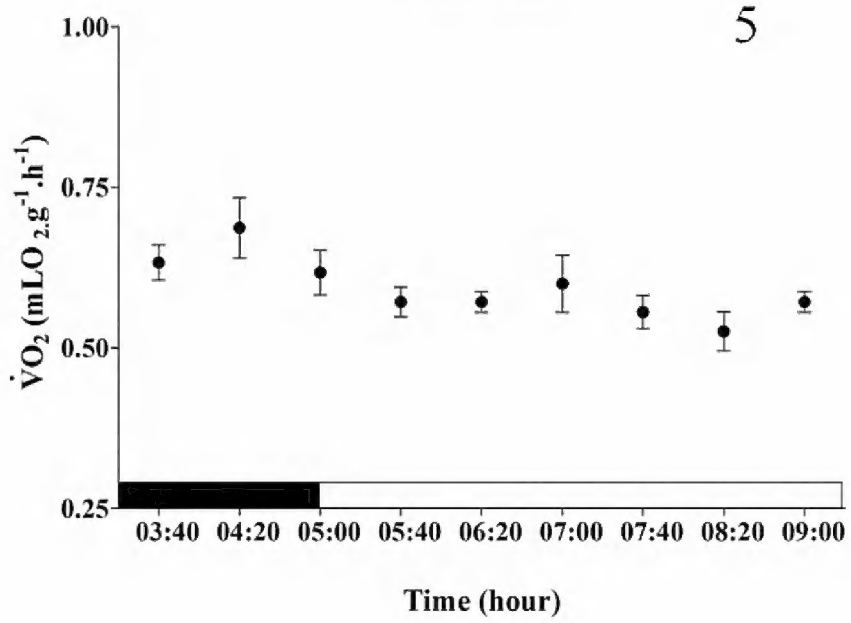
The lowest metabolic rate of *T. setosus* was 0.60 ± 0.01 $mLO_2.h^{-1}.g^{-1}$ at 32 °C (Fig. 1). The best fitting model gave the lower limit of the thermoneutral zone at T_a = 25.7 °C. Effect of T_a on $\dot{V}O_2$ below the thermoneutral zone was described by segmented regression as $\dot{V}O_2$ ($mLO_2.h^{-1}.g^{-1}$) = -0.018.T_a + 1.06. The

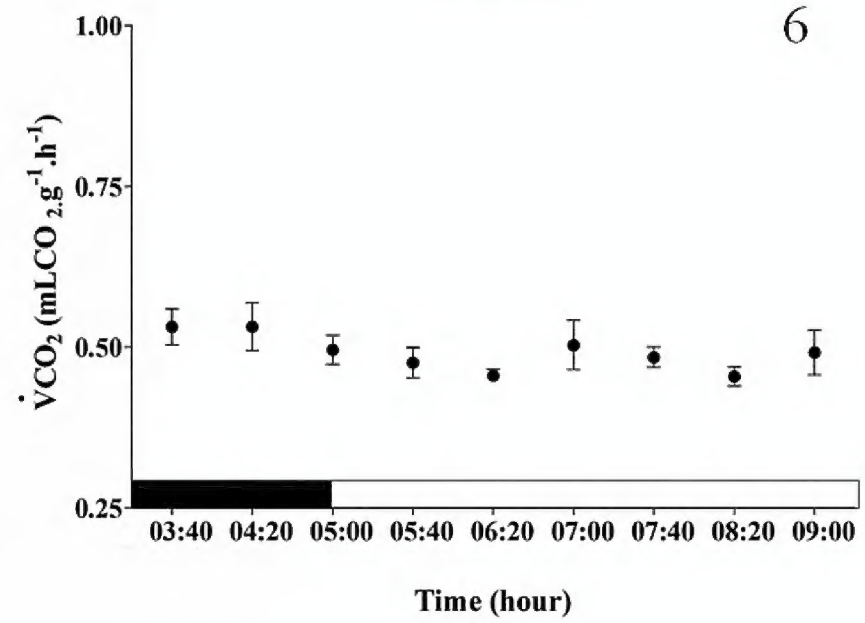












Figures 1–6. Relationship between O_2 consumption ($mLO_2.g^{-1}.h^{-1}$) and environmental temperature (°C) in *T. setosus* (1) and *C. bishopi* (2), as well as relationship between O_2 consumption ($mLO_2.g^{-1}.h^{-1}$) and time of day in *T. setosus* (3) and *C. bishopi* (5) and relationship between CO_2 production ($mLCO_2.g^{-1}.h^{-1}$) and time of day in *T. setosus* (4) and *C. bishopi* (6). Bars indicate the respective phase of the inverted photocycle, dark (black) or light (white). Values represent mean and standard error (mean ± SE)

mean of $\dot{V}O_2$ at minimum T_a of 20 °C was 0.71 ± 0.06 $mLO_2.h^{-1}.g^{-1}$ and at the maximum T_a of 40 °C was 0.84 ± 0.06 $mLO_2.h^{-1}.g^{-1}$, representing 116 % and 138 % of the $\dot{V}O_2$ of the thermoneutral zone, respectively.

Clyomys bishopi's lowest metabolic rate was found at 32 °C with 0.62 ± 0.02 $mLO_2.h^{-1}.g^{-1}$ (Fig. 2). The lower limit of the thermoneutral zone was found at T_a = 29.3 °C. The increase of $\dot{V}O_2$ due to decreasing T_a can be described as $\dot{V}O_2$ ($mLO_2.h^{-}$

$^{1}.g^{-1}$) = -0.042.T_a + 1.86. The mean of $\dot{V}O_2$ at minimum T_a of 20 °C was 1.03 ± 0.15 $mLO_2.h^{-1}.g^{-1}$ and at the maximum T_a of 36 °C was 1.11 ± 0.33 $mLO_2.h^{-1}.g^{-1}$, representing 156% and 179% of $\dot{V}O_2$ of the thermoneutral zone, respectively. $\dot{V}O_2$ at T_a of 40 °C was not obtained because the first tested animal was not able to survive at this T_a, and therefore we refrained from exposing the other animals to 40 °C.

Trinomys setosus' lowest metabolic rate measurements during the animal's dark and light phase were found at 04:20 am (0.76 ± 0.04 $mLO_2.h^{-1}.g^{-1}$) and 07:00 am (0.56 ± 0.02 $mLO_2.h^{-1}.g^{-1}$), respectively (Fig. 3). $\dot{V}O_2$ was lower in the light phase than in the dark phase (p = 0.01) and did not vary within the light phase (p = 0.19); therefore the mean $\dot{V}O_2$ of the light phase at 32 °C was $\dot{V}O_2$ = 0.61 ± 0.04 $mLO_2.h^{-1}.g^{-1}$. The same pattern was observed for $\dot{V}CO_2$ (Fig. 4), the lowest $\dot{V}CO_2$ being found during the light phase at 07:00 am (0.46 ± 0.03 $mLCO_2.h^{-1}.g^{-1}$) and not varying within the light phase (p = 0.38), resulting in a mean $\dot{V}CO_2$ during the light phase of 0.49 ± 0.03 $mLCO_2.h^{-1}.g^{-1}$. RER (0.81 ± 0.04) remained constant throughout the light phase (p = 0.48).

Clyomys bishopi's lowest metabolic rate measurements during the animal's dark and light phase were found at 03:40 am (0.63 ± 0.03 $mLO_2.h^{-1}.g^{-1}$) and 08:20 am (0.53 ± 0.03 $mLO_2.h^{-1}.g^{-1}$), respectively (Fig. 5). $\dot{V}O_2$ was lower during the animals light phase than the dark phase (p = 0.02) and did not vary within the light phase (p = 0.39), giving a mean $\dot{V}O_2$ of the light phase at 32 °C as 0.57 ± 0.03 $mLO_2.h^{-1}.g^{-1}$. An identical pattern was observed for $\dot{V}CO_2$ (Fig. 6), the lowest $\dot{V}CO_2$ being found in the animals light phase at 08:20 am (0.45 ± 0.02 $mLCO_2.h^{-1}.g^{-1}$), without variation within the light phase (p = 0.62), giving a mean $\dot{V}CO_2$ for the light phase of 0.48 ± 0.02 $mLCO_2.h^{-1}.g^{-1}$. RER (0.84 ± 0.04) remained constant during the light phase (p = 0.70).

DISCUSSION

The intervals for the thermoneutral zones obtained in the present study are in accordance with data available for other caviomorph terrestrial rodents such as *O. degus* (27–35 °C), *Thrichomys apereoides* Lund, 1839 (25–35 °C), *Chinchilla laniger* Bennett, 1829 (22–35 °C), *Dazyprocta azarae* Lichtenstein, 1823 (18–35 °C) (Arends and Mcnab 2001) and fossorial rodents such as *Ctenomys talarum* Thomas, 1898 (25–35 °C) (Bush 1989). *Trinomys setosus* showed a relatively broad thermoneutral zone with a lower limit at T_a = 25.7 °C extending at least to T_a = 32 °C (Fig. 1), which is compatible with its environment's mean T_a = 25 °C (Hijmans et al. 2005). The increases of metabolic rate below (116%) and above (138%) the limits of the thermoneutral zone were small in comparison to other caviomorph rodents such as *C. laniger* and *O. degus* (Arends and McNab 2001), however measurements in lower temperatures could reveal that these animals may be more affected by a lower T_a.

Clyomys bishopi showed a narrow thermoneutral zone with its lower limit at T_a = 29.3 °C extending to T_a = 32 °C (Fig. 2), which is higher than its mean environmental T_a of 20 °C (Hijmans et al. 2005). However, it is possible that the thermoneutral zone in this species is not related to above ground T_a, but to the amplitude in burrow temperature (Burda et al. 2007). *Clyomys bishopi*'s metabolic rate was more affected by experimental temperatures below (156%) and above (179%) the limits of the thermoneutral zone. Moreover, *C. bishopi* seems not be able to cope well with experimental T_a = 40 °C, since mortality was observed in the only tested animal at T_a = 40 °C. *Ctenomys talarum* shows a broader thermoneutral zone (25–35 °C) than *C. bishopi*, but this species was also not able to survive temperatures above its thermoneutral zone at T_a = 40 °C (Bush 1989). Such a thermoregulatory constrain may be expected in fossorial rodents as long as burrow temperature variation is predictable and animals are able to use behavioral strategies to avoid overheating, i.e. timing their digging activity according to burrow temperatures or moving to cooler parts of the burrow (Burda et al. 2007). Moreover, it is known that other fossorial rodents will be exposed to only small temperature variations inside burrows (McNab 1966, Baldo et al. 2015). Further studies could address daily and annual temperature ranges within burrows and evaluate the whole set of behavioral strategies to cope with temperature variation.

The majority of echimyids forage during the dark phase (Emmons and Feer 1997) and, as expected, *T. setosus* and *C. bishopi* showed the lowest metabolic rates during the light phase. The variation observed in metabolic rate of *T. setosus* is compatible with a nocturnal species with its circadian cycle entrained to day-night phases (Fig. 3) (Koukkari and Sothern 2006). The same pattern has been observed in another species of the same genus, *Trinomys yonenagae* Rocha, 1995 (Marcomini and Spinelli 2003). Concurrently, although *C. bishopi* presented the lowest metabolic rate during the light phase and is usually not seen on the surface during the day, the metabolic rate variation through time does not provide strong evidence that *C. bishopi* is nocturnal (Fig. 5). Still, it is possible that this species presents a circadian cycle entrained to light and dark phases or synchronized with ambient temperature (Šklíba et al. 2014), food availability (Nelson et al. 1975) or social environment (Crowley and Bovet 1980). Field data on activity patterns are needed to clarify which environmental cues could be regulating *C. bishopi* activity under natural conditions. The absence of variation in RER values was expected as no change in metabolic fuel use (i.e., carbohydrates, lipids or proteins) was imposed and RER values were compatible with animals in a post-absorptive state, during which mixed fuels are generally used (Wang et al. 2006).

BMR data of these species are important due to the poor representation of the Echimyidae family in other physiological studies. Echimyidae include 95 species of rodents distributed in 21 genera, however, only few data are available regarding metabolic rate (Table 1). Moreover, some species' metabolic rate was measured with no consideration of ambient temperature and circadian effects, which is not compatible with BMR conditions (Hulbert and Else 2004, Connolly and Cooper 2014). BMR of

Table 1. Available data of metabolic rate for Echimyidae species.

	Body mass (g)	Metabolic rate ($mLO_2.h^{-1}.g^{-1}$)	Reference
Clyomys bishopi[b]	343.2	0.53	This work
Trinomys setosus[b]	316.6	0.56	This work
Trinomys yonenagae[a]	137.6	0.63	Barros et al. (1998)
Trinomys iheringi[a]	223.9	0.83	Barros et al. (1998)
Proechimys semispinosus[b]	498.0	0.63	Arends and McNab (2001)
Thrichomys apereoides[b]	323.0	0.64	Arends and McNab (2001)
Myocastor coypus[b]	4325.0	0.70	Segal (1978)

[a]RMR conditions, [b]BMR conditions.

C. bishopi and *T. setosus* were both lower than predicted by body mass when applying Kleiber's regression of BMR ($kcal.day^{-1}$) = $73.3 \times M_B^{0.74}$ (Kleiber 1932), representing 68% and 70% of the predicted values, respectively. When applying the allometric regression given by McNab (2008) for rodents, BMR ($mLO_2.h^{-1}$) = $3.87 \times M_B^{0.71}$, *C. bishopi* and *T. setosus* BMRs are equivalent to 76 % and 79 % of predicted values, respectively. Usually such reduction in metabolic rate would be attributed to fossoriality. However, as *T. setosus* is a terrestrial species, this result does not support the hypothesis of reduced BMR being related to fossoriality.

Our results illustrate the apparent complexity of traits influencing BMR in this group. It is possible that the reduced basal metabolic rate for both species may be explained by a phylogenetic effect as suggested for some echimyids (Roberts et al. 1988) or by climatic variables such as high ambient temperature during these species evolution (Lovegrove 2003). In any case, additional data and broader comparisons are needed to understand BMR variation within Echimyidae species.

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